

MELANISM IN *PHIGALIA TITEA* (CRAMER)
(LEPIDOPTERA: GEOMETRIDAE) IN SOUTHERN
NEW ENGLAND: A RESPONSE TO
FOREST DISTURBANCE?

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Abstract.—The typical and melanic morphs of *Phigalia titea* (Cramer) exhibited different background preferences in an experimental apparatus, the typicals behaving like species known to rest on many tree species in nature, and the melanics behaving like species known to rest preferentially on white birches. Field observations of *Cosymbia pendulinaria* Guenée indicate that some melanic moths are cryptic on gray (*Betula populifolia*) and paper (*B. papyrifera*) birches. It is suggested that the successional characteristics of these birches in New England forests may provide the basis for a recurring advantage of melanism, and that increases in the abundance of these birches since colonial settlement may explain the melanism seen in the region today.

Industrial melanism in moths has become a standard textbook example of evolution in action. The traditional explanation of this phenomenon was developed by Kettlewell and his associates working in England with the peppered moth, *Biston betularia* (L.). This explanation involves a series of observations including well-documented changes in the frequencies of the melanic morphs of this species, a simple genetic basis for the melanic condition, an environmental change (darkening of tree trunks) to which the moths are apparently responding, and a selective agent (birds preying on resting moths) which presumably directs the evolutionary process (Kettlewell, 1955a, 1956, 1973). Recently, however, increasing skepticism as to the general adequacy of this explanation has emerged (Bishop, 1972; Creed et al., 1973; Sargent, 1974; Bishop and Cook, 1975; Lees and Creed, 1975; Steward, 1977a, b; Lees, 1981; Hailman, 1982), based in part on reports of rural melanism in North America (Klots, 1964, 1966, 1968a, b; Sargent, 1971, 1974, 1983; Jones, 1977; West, 1977; Manley, 1981). A particular problem is posed by experimental results which indicate that melanic individuals of several species prefer light over dark backgrounds (Sargent, 1968, 1969; Lees, 1975; Steward, 1976, 1977c), unlike the dark over light background preference reported in similar experiments with melanic *B. betularia* (Kettlewell, 1955b; Boardman et al., 1974; Kettlewell and Conn, 1977).

The present paper reports results of further background preference tests with *Phigalia titea* (Cramer) (Lepidoptera: Geometridae), a species whose melanic morph has previously been shown to prefer white over black backgrounds (Sargent, 1969). These new results indicate that melanic *P. titea*, unlike their typical counterparts, behave like species that are known to rest on white birches (*Betula papyrifera* Marshall and *B. populifolia* Marshall) in nature. These experimental findings, together with field observations of the birch-resting geometrid, *Cosymbia pendulinaria* Guenée, suggest

that melanic moths may be cryptic on very light trees like birch and aspen because of the numerous black patches which also characterize these trees.

White birches and aspens are early, successional species in New England forests and I suggest that natural disturbances that favor these trees may have provided recurring opportunities for the rise and spread of melanism in moths in the past. It follows that the extensive human disturbance of the forest since colonial settlement could be a factor in the incidence of melanism we see today.

METHODS AND MATERIALS

The experimental apparatus used in this study is similar to one used previously in black vs. white background preference tests (Sargent, 1968, 1969a, b, 1973; Lees, 1975), but here consisted of four backgrounds: white, black, horizontally striped, and vertically striped. Each of the four backgrounds was made from a piece of white blotting paper, unmarked to provide the white background, and marked with a black marking pen to provide the striped and black backgrounds. The striped backgrounds consisted of repeating sequences of 0.5 mm, 2.0 mm, and 10.0 mm black lines, the lines separated from one another by 7.0 mm white spaces (the backgrounds overall being 65% white and 35% black). The four pieces of blotting paper were formed into a cylinder of alternating solid and striped backgrounds, and this cylinder was set into a plywood box (35.6 cm square by 48.3 cm high) which was covered with a pane of clear window glass. The entire apparatus was set out in a wooded area near my home in Leverett, Massachusetts.

The moths to be tested were captured during the seasons of 1981–1983 at 150-watt incandescent spotlights (Westinghouse outdoor projector) or a 15-watt fluorescent blacklight tube (General Electric F15T8 BL). The moths were placed into the experimental apparatus after their capture at night, and their background selections were recorded shortly after daybreak on the following morning.

The statistical test used in all comparisons of background selections in this apparatus was the $R \times C$ test of independence using the G-test (Sokol and Rohlf, 1969).

Phigalis titea is an early spring species, with males on the wing in Leverett during March and April (females have rudimentary wings and do not fly). Typical *P. titea* are light gray with strongly contrasting black lines, while melanics are evenly blackish overall (both morphs are illustrated in Remington (1958) and Sargent (1983). The melanic morph, "deplorans," was named in 1938 (Franclemont), though an early specimen was described in 1869 (Minot). Owen (1961, 1962) has discussed the history of melanism in this species, noting that early records of the melanics were not concentrated near industrial centers. Lees (1971) has made a similar point regarding melanism in the closely related *P. pilosaria* Schiff. in England. In Leverett, melanics have comprised 18.8% of the 4,078 male *P. titea* captured over the past 16 years (Sargent, 1983).

RESULTS AND DISCUSSION

The typical and melanic morphs of *P. titea* exhibited significantly different background preferences in the present experimental apparatus, the typicals preferring the horizontally and vertically striped backgrounds, and the melanics preferring the horizontally striped and white backgrounds ($P < 0.05$) (Fig. 1).

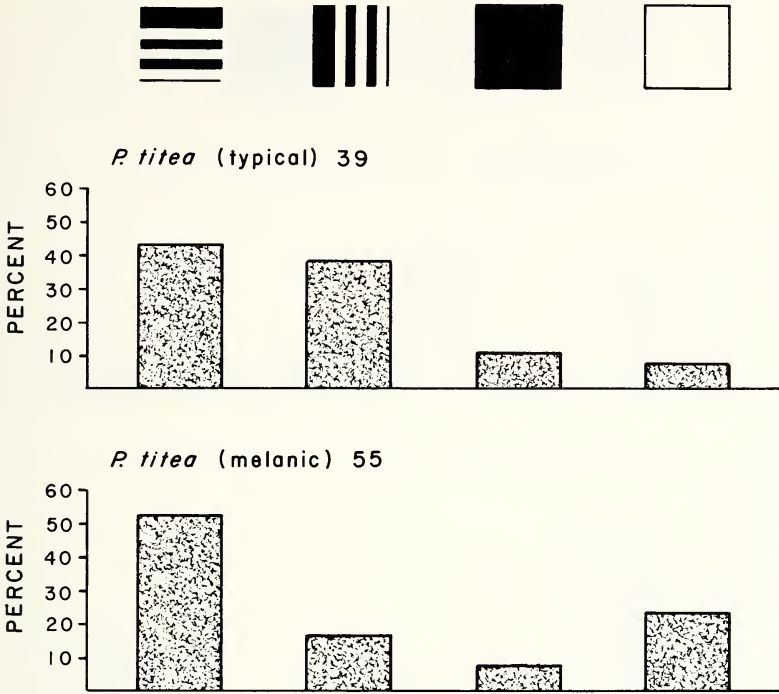


Fig. 1. The distribution of typical and melanic *Phigalia titea* in an experimental apparatus providing a choice among horizontally striped, vertically striped, black, and white backgrounds. The numbers of individuals tested are given after the morph designations.

The behavior of the typical *P. titea* was similar to that of a number of light, bark-like geometrids that are known to rest by day on the trunks of a wide variety of tree species in the Leverett area (Sargent and Keiper, 1969; Sargent, unpubl.). The background choices of one such species, *Anacamptodes ephyraria* (Walker), are depicted in Figure 2, and these did not differ from those of the typical *P. titea* ($P > 0.90$). The behavior of the melanic *P. titea*, on the other hand, resembled that of several very pale geometrids that prefer to rest by day on white birches (Sargent and Keiper, 1969; Sargent, unpubl.). *Cladara atroliturata* (Walker) is one such species, and its background selections in the experimental apparatus (Fig. 2) did not differ from those of the melanic *P. titea* ($P > 0.30$).

These experimental results suggest that the two morphs of *P. titea* might differ with respect to their resting habits in nature. Unfortunately, as with many species exhibiting melanism (Mikkola, 1979), there are no published observations of *P. titea* in natural resting situations. I have been unable to find individuals of either morph at rest in the Leverett area, though my searches to date have concentrated on oaks, as I have received one report of typical *P. titea* resting on *Quercus alba* L. in southwestern Massachusetts (R. D. Childs, pers. comm.). The possibility of a birch-resting preference for the melanics had not occurred to me prior to the present analysis, though this possibility should guide future search efforts.

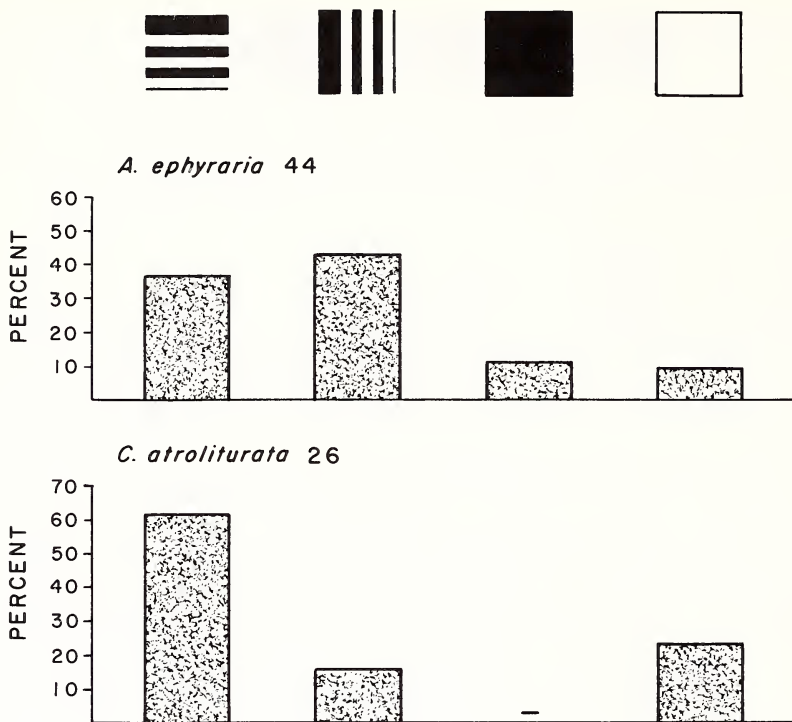


Fig. 2. The distribution of *Anacamptodes ephyraria* and *Cladara atroliturata* in an experimental apparatus providing a choice among horizontally striped, vertically striped, black, and white backgrounds. The numbers of individuals tested are given after the species names.

I have found many specimens of another local geometrid, *Cosymbia pendulinaria* Guenée, resting on white birches (Sargent and Keiper, 1969; Sargent, unpubl.), and further consideration of this species may be informative. *Cosymbia pendulinaria* is double-brooded in Leverett, but has a later flight season (May–August) than *P. titea*. The moth is typically white with variable amounts of blackish dusting, but occurs as well in a melanic morph, “nigricaria” (Rothke, 1920), which is very dark gray or blackish. This melanic morph comprises about 5% of the species population in Leverett.

Both morphs of *C. pendulinaria* prefer white over black backgrounds in experimental tests (Sargent, 1968); and in the present apparatus, both exhibited similar preferences ($P > 0.80$) for the horizontally striped and white backgrounds (Fig. 3). Their behavior in this apparatus was similar then to that of the birch-resting *C. atroliturata* (P 's > 0.10 and > 0.30 for the typical and melanic morphs respectively) and to the melanic *P. titea* (P 's > 0.30 and > 0.50 for the typical and melanic morphs, respectively), but differed significantly from the typical *P. titea* (P 's < 0.01 for both morphs).

My field observations indicate that both morphs of *C. pendulinaria* rest prefer-

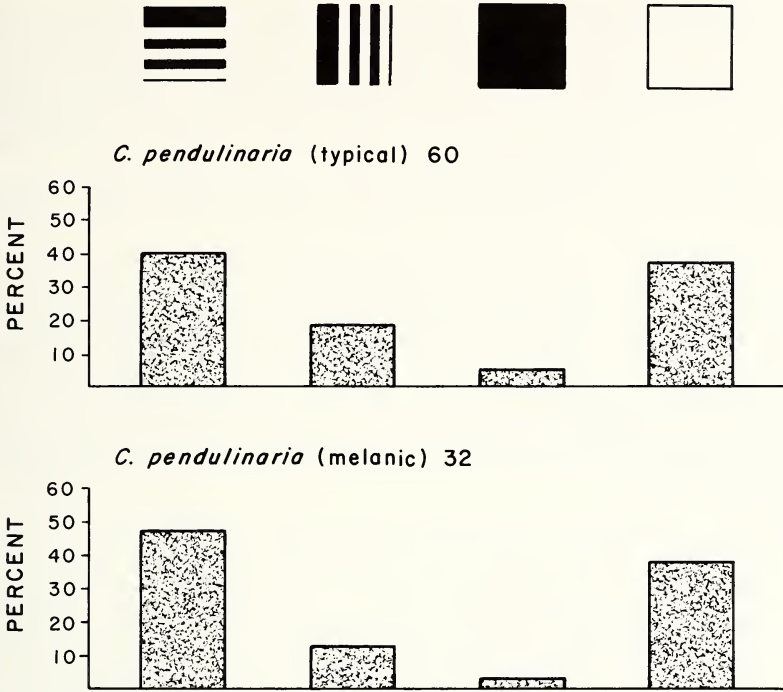


Fig. 3. The distribution of typical and melanic *Cosymbia pendulinaria* in an experimental apparatus providing a choice among horizontally striped, vertically striped, black, and white backgrounds. The numbers of individuals tested are given after the morph designations.

entially on white branches (ca. 98% of over 200 observations of typicals, and all 13 observations of melanics). Both morphs appear cryptic on these trees, though for different reasons. Typicals tend to match the predominantly white backgrounds that these birches provide; and melanics, though conspicuous with respect to their immediate surroundings, tend to resemble the black patches that characterize these trees, when viewed from a more distant perspective. Some melanic *C. pendulinaria* (5/13) were found abutting black patches on birches, and this positioning seemed to enhance the moths' crypsis by disrupting their outlines and making them appear as irregular extensions of the black patches with which they were associated. There is some evidence for a similar tendency in *Phigalia pilosaria*, in that both morphs of this species show a highly significant tendency to rest with their heads exactly at the black boundary when tested in a black vs. white background choice apparatus (Lees, 1975).

The results of the present study suggest that some melanic moths may be adapted to exploit white backgrounds that are variegated with black, rather than the uniformly dark or black backgrounds that are suggested by the traditional explanation of industrial melanism. In New England, the trees that most clearly provide such white and black variegated backgrounds are the two common white birches, paper birch

(*Betula papyrifera*) and gray birch (*B. populifolia*). Both of these trees have chalky white bark with prominent, triangular black patches (these patches being especially common on *B. populifolia*) (Harlow et al., 1978). (The aspens, *Populus tremuloides* Michx. and *P. grandidentata* Michx. have similar, though less strikingly variegated bark surfaces, and a case for their role in the maintenance of melanic polymorphisms in moths might also be developed.)

Betula papyrifera and *B. populifolia* are relatively short-lived, shade intolerant species which exhibit the "exploitative strategy" in forest succession, persisting for only a single generation (ca. 35 years in the case of *populifolia*, and ca. 75 years in the case of *papyrifera*) in undisturbed situations (Harlow et al., 1978; Bormann and Likens, 1979). Pollen and seed data indicate that both species have been present in New England for at least 10,000–12,000 years, and that natural disturbances (e.g., hurricanes, fires) have intermittently provided locally favorable conditions for their occurrence (Patterson, unpubl.). However, neither species seems to have been common in the so-called climax forests that characterized much of New England prior to the arrival of Europeans in the 17th and 18th centuries (Bromley, 1935; Siccama, 1971; Lorimer, 1977).

Since colonial settlement there has been a substantial increase in the frequencies of these birches in response to man's disturbance of the forests (clearing, logging) and his subsequent abandonment of agricultural lands (Harlow et al., 1978; Bormann and Likens, 1979). Palynological documentation of this increase is clearest for gray birch (*B. populifolia*), since this species can be separated from other *Betula* on the basis of its small pollen size (Leopold, 1956; Patterson, unpubl.). A trend of increasing abundance of gray birch since local settlement characterizes pollen records throughout central and southern New England, and it seems safe to conclude that gray birch is more abundant there today than at any other time in the past 1,000 years (Patterson, unpubl.).

If melanism in some moth species is a response to the availability of suitable resting sites provided by white birches, then the recent increase in the abundance of these trees may provide an explanation for the corresponding increase in the incidence of melanism. Furthermore, the transitory characteristics of these early successional tree species would provide the basis for a recurring adaptive advantage of the melanic condition. It is widely recognized that some sort of recurring advantage is implied by the fact that melanism in moths is almost always a dominant trait (Kettlewell, 1973; Ford, 1975; Hailman, 1982).

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